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Lateralization of spontaneous behaviours in the domestic cat, *Felis silvestris*

McDowell, L. J., Wells, D. L., & Hepper, P. G. (2018). Lateralization of spontaneous behaviours in the domestic cat, *Felis silvestris*. *Animal Behaviour*, 135, 37-43.

Published in:
Animal Behaviour

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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4 **Lateralisation of spontaneous behaviours in the domestic cat, *Felis silvestris***

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8 Running Headline: McDowell et al.: Lateralised behaviour in cats

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ABSTRACT

Recent years have drawn attention to the link between lateral bias and cerebral functional asymmetry in animals. Most studies of animal laterality have focused on limb use arising from forced experimental challenges as opposed to spontaneous behaviours. This study explored, for the first time, the expression of lateralised spontaneous behaviour in the domestic cat, a species that exhibits motor bias in the form of paw preferences. The side used by 44 pet cats to perform three spontaneous behaviours (lying side, stepping down a flight of stairs, stepping over a raised object) was recorded. Paw preferences were also assessed using a more traditional forced food reaching challenge. Cats showed a significant lateral bias for food reaching (73%), stepping down (70%) and stepping over (66%). Paw-preferent animals, however, did not differ significantly in their tendency towards left- or right-sideness. The direction of the cats' side preferences was significantly correlated for most of the measures, whether forced or spontaneous. The strength of the cats' motor bias was significantly related to task; animals displayed a weaker lateral bias for lying side than any of the other measures. The study revealed a sex split in the direction, although not the strength, of the cats' lateral bias for food reaching, stepping down and stepping over. Male animals showed a significant preference for using their left paw on these measures, while females were more inclined towards right-sideness. The study provides the first evidence that the domestic cat displays motor laterality on specific spontaneous behaviours, and that the direction, although not the strength, of these lateral biases is largely consistent with that of an experimental task. The results suggest that the more forced food reaching test traditionally used to assess motor bias in the cat offers a biologically valid measure of limb use in this species.

Keywords: behaviour; cats; handedness; laterality; paw preferences; sex differences

INTRODUCTION

One of the most prevalent features of human behaviour is motor laterality, defined as the preferred use of one limb over another (e.g., Harris, 1983; Springer & Deutsch, 1989). The most obvious display of motor bias in humans is handedness. An estimated 90% of people prefer to use their right hand for most activities, including tool-use, teeth brushing and writing (Annett, 1985; Porac & Coren, 1981).

It was previously believed that lateralised behaviour was a uniquely human trait. Research now indicates, however, that many species of animal (e.g., amphibians, rodents, cats, primates, marsupials, whales) display lateralised motor behaviours. This has led to suggestions that lateral bias may be a universal phenomenon (for reviews see Frasnelli, Vallortigara & Rogers, 2012; MacNeilage, Rogers & Vallortigara, 2009; Rogers, 2002; Rogers, Vallortigara & Andrew, 2013; Vallortigara, Chiandetti & Sovrano, 2010; Vallortigara & Rogers, 2005), although whether this exists at the level of group in animals, or is related to other aspects of brain asymmetry, is still unclear (see reviews by Corballis, 2009; Rogers, 2009; Vallortigara & Versace, 2017; Versace & Vallortigara, 2015).

Studies in the area of animal laterality have typically focused their attention on experiments involving forced tasks, notably food reaching. However, a smaller number of investigations have explored the directionality of more spontaneous expressions of animal behaviour. Studies have focused on behaviours including the side used for foraging and feeding (gorillas- Byrne & Byrne, 1991; Tabiowo & Forrester, 2013; humpback whales- Canning et al., 2011; Clapham, Leimkuhler, Gray & Mattila, 1995; Woodward & Winn, 2006; walruses- Levermann, Galatius, Ehlme, Rysgaard & Born, 2003), the limb employed to initiate movement (horses- Lucidi et al., 2013; McGreevy & Rogers, 2005; giraffes- Svoke, 2017;

76 dogs- Hackert, Maes, Herbin, Libourel, & Abourachid, 2008; Tomkins, Thomson, &
77 McGreevy, 2010), grooming (chimpanzees- Marchant & McGrew, 1996), infant cradling
78 (chimpanzees- Manning & Chamberlain, 1994; Toback, 1999), clapping (chimpanzees-
79 Fletcher, 2006), suckling (horses- Komarkova & Bartosova, 2013; zebra- Pluhacek al. 2013),
80 hemifield use (birds- Ventolini, Ferrero, Sponza, Chiesa, Zucca & Vallortigara, 2005),
81 turning behaviour (sheep- Versace, Morgante, Pulina & Vallortigara, 2007), ground
82 scratching (chicks- Tommasi, 1999), and even urination (dogs- Gough & McGuire, 2015).
83 Many, although not all, of these studies suggest that lateral biases can be recorded
84 successfully from naturalistic observations of animal behaviour. What is less apparent is
85 whether these biases are consistent with those recorded experimentally using more forced
86 limb reaching tasks. Indeed, only a small number of studies, all involving primates
87 (Campbell's monkeys- Chapelain, Bec & Blois-Heulin, 2006, Chapelain et al., 2012; red-
88 capped mangabeys- Chapelain et al., 2012; red-fronted lemurs, Schnoell, Huebner, Kappeler
89 & Fichtel, 2014 common marmosets- Hook & Rogers, 2008;), have compared motor
90 preferences using these two methodological approaches. Two of the studies (Chapelain et al.,
91 2006; Schnoell et al., 2014) found that the expression of manual laterality was weaker in
92 naturally occurring behaviours (e.g., holding branches, self-grooming, feeding) compared to
93 forced limb use on an experimental task. Such findings are in line with the hypothesis
94 proposed by Warren (1980) which states that hand preferences should be stronger and more
95 rigid in experimental conditions on the basis that laterality is an artificial phenomenon
96 created by such situations. Moreover, Schnoell and others (2014) argue that a strong manual
97 bias for spontaneous actions may not be ecologically relevant for some species, particularly if
98 both hands are needed to ensure health and safety, e.g., swinging across trees. Nevertheless,
99 it seems that studying manual preferences on both experimental tasks and spontaneous
100 behaviours may provide more realistic and ecologically valid insights into the evolution and

significance of lateral biases in an animal's daily life than the use of only one methodological approach.

The following study explored the expression of lateralised spontaneous behaviour in the domestic cat, *Felis silvestris*, a species that has been shown to exhibit motor bias in the form of paw preferences (e.g., McDowell, Wells & Hepper, 2016; Pike & Maitland, 1997; Wells & Millsopp, 2009, 2012). We recorded the limb or side used by 44 pet cats to perform three spontaneous (i.e., unforced) behaviours (lying side, stepping down a flight of stairs, stepping over a raised object). Each animal's paw preferences were also assessed using a more traditional forced food reaching challenge (McDowell et al., 2016). The study aimed to identify whether asymmetries are consistent using two methodological approaches and determine whether spontaneous expressions of natural behaviour can be used as a reliable indicator of cerebral asymmetry in the cat.

METHODS

Subjects

Forty-four neutered pet cats (24 male, 20 female), of mixed breed, aged between 1-17 years (mean age=3.98 +/- 0.56 years), participated in the study. For the purpose of analysis (see later), the age of the cats was categorised as ‘young’ (defined as animals between 1-6 years of age) and ‘old’ (defined as animals between 6-17 years of age). There was no significant difference in the distribution of male and female animals in the two age groups ($\chi^2_1=3.26$, $p=0.08$). All of the cats were family pets whose owners had consented to them participating in the study. None of the cats had undergone any behavioural training, nor had any disability or behavioural problem preventing them from completing the study.

Laterality measures

Cats’ lateral preferences were assessed using two approaches, namely, an experimental food reaching test and observations of 3 spontaneous behaviours:

Food reaching test

Cats’ paw preferences for food reaching were assessed using the Catit Senses Food Maze (Catit, UK). This maze is a 35.6cm tall spherical feeding ‘tower’, comprising 3 levels into which food can be placed. The food is accessed via 3 holes on each level (see Figure 1 and <https://www.catit.com/uk/shop/senses-2-food-tree>). For the purpose of this study, the top level of the food maze was removed as it proved too high for the cats to put their paws into without standing on their rear legs and compromising balance. The Catit has been used successfully to record cats’ paw preferences (McDowell et al., 2016), and demonstrates good test-retest reliability (McDowell, 2017).

140

141 (Figure 1 about here)

142

143 Spontaneous behaviours

144 Three spontaneous behaviours were recorded:

145 i) *Lying side*

146 Lying side has been studied as a measure of lateral bias in quadrupedal species including
147 dairy cattle (e.g., Tucker, Cox, Weary & Spinka, 2009) and sheep (Lane & Phillips, 2004).
148 Cats typically lie on one side of their body while resting or sleeping. For this study, owners
149 were required to record whether their cat lay down on their left or right side for each
150 occurrence of this behaviour.

151

152 ii) *Step down*

153 The “First-stepping” task has been used to successfully measure paw preference in dogs
154 (Tomkins et al., 2010). For this study, owners were required to record the paw (left or right)
155 first used by their pet to descend their indoor set of stairs.

156

157 iii) *Step over*

158 Many cats use a litter tray for urination and/or defecation (Crowell-Davis, Curtis & Knowles,
159 2004). As this is often a tray with a slightly raised perimeter, the cat must lift one of its
160 forelimbs to step into it. For the purpose of this study, owners were therefore required to
161 record the paw first used by their cat to enter their litter tray.

162

163 To ensure familiarity with the three spontaneous behaviours and increase the objectivity of
164 measures between subjects, the cats’ owners were provided with an information sheet

describing the actions they should expect to witness in their pet. Any spontaneous occurrences of the behaviours made by the subject cats were also pointed out to the owners at the time of the Experimenter's visit to their homes. In addition, pictures depicting cats showing the three activities were presented to the owners. It was made clear that an animals' use of both paws simultaneously should not be recorded. Owners were contacted once a week to ensure compliance with the protocol and address any concerns.

Procedure

All of the subjects were tested individually in their own home environment. Each cat was initially required to undertake the experimental *food reaching* test. Prior to the start of the first trial, the cat was shown, and allowed to sniff, the food treat (Dreamies, Mars Petcare, UK - small squares of cheese flavored cat treats). As the cat watched, 10 treats were placed on the top (i.e., second) level of the food maze. Since the food could be accessed through 3 holes, it was ensured that the cat was placed directly in front of one hole for each trial. As and when required (i.e., once all the food treats had been accessed by the cat), another 10 treats were placed in the food maze. A single trial comprised the cat placing its paw inside the food maze and attempting to remove the treat. Only once the paw had been removed from the maze did the next trial begin. The paw the cat used to attempt food retrieval, regardless of whether or not a treat was retrieved, was recorded. Testing was carried out on a daily basis until 50 responses were made. An average of 15 trials were carried out by each cat every day to avoid the animals becoming bored, tired or stressed. No reward, be it tactile (comforting, stroking) or social (verbal praise or smiling), was provided during the task.

Laterality data on the cats' spontaneous behaviours were collected by the subjects' owners over a period of 3 months. Owners were given a score sheet and asked to record each

occurrence of the 3 spontaneous behaviours outlined above. The occurrence of 50 (left plus right) expressions of each of the three spontaneous behaviours (*lying side, step down, step over*) was recorded for each subject. Between 15-20 occurrences of each behaviour were recorded per month by each cats' owner. Data were collected over a range of observation sessions (e.g., in the morning, afternoon and evening) for each animal to reduce the likelihood of interference from either one-off, or very habitual, events.

Statistical Analysis

Fifty data points per animal were recorded for each of the laterality measures (*food reaching, lying side, step down, step over*). Binomial z -scores were calculated to determine whether the frequency of right- or left-side use exceeded that expected by chance for each of the measures. An alpha value of 0.05 was adopted for all analyses. A z -score greater than +1.96 (two-tailed) reflected a significant left paw preference, whilst a z -score less than -1.96 indicated a significant right paw preference. Cats with z -scores between +1.96 and -1.96 were classified as ambilateral.

A directional handedness index (HI) was calculated (see Wells, 2003) to quantify each cat's lateral preference for each measure on a continuum from strongly left-side preferent (+1) to strongly right side-preferent (-1). The HI was calculated by dividing the difference between the total number of left and right side uses by their sum $(L-R)/(L+R)$. A mixed-design ANOVA for the between-subjects factors of feline sex (*male, female*) and age (*young, old*) and the within-subjects factor of task (*food reaching, lying side, step down, step over*) was carried out to determine whether the direction of the cats' side preferences differed between the tasks or was influenced by the animals' sex or age.

The strength of the cats' lateral preferences was calculated by taking the absolute value of each HI score (ABS-HI) for each measure. A mixed-design ANOVA for the between-subjects factors of feline sex (*male, female*) and age (*young, old*) and the within-subjects factor of task (*food reaching, lying side, step down, step over*) was carried out to determine whether the strength of the cats' side preferences differed between the tasks or was influenced by the animals' sex or age.

Finally, Pearson product moment correlations were conducted to compare both the direction (HI scores) and strength (ABS-HI scores) of lateral bias across the four tasks to explore for any consistencies in strength and/or direction of motor asymmetry.

Ethical Note

All methods adhered to the Association for the Study of Animal Behaviour/ Animal Behavior Society Guidelines for the Use of Animals in Research (Association for the Study of Animal Behaviour, 2006). Ethical approval for the study was granted by the Research Ethics Committee, School of Psychology, QUB. All of the cats' owners were required to complete a written consent form at the time of subject recruitment. Owners were fully informed in writing of the study's purpose and advised that they were free to leave the project and have their pets' data withdrawn at any time. To minimise stress to the cats, data were collected in the subjects' own homes. Animals' paw preferences on the food reaching test were collected over an average of 3 days to minimise the risk of inducing tiredness or stress.

RESULTS

Distribution of lateral bias

Food reaching

The distribution of the cats' paw preferences on the food reaching test was not significantly different to that expected by chance alone ($\chi^2_2=1.27$, $P=0.53$). Significantly ($P=0.003$, binomial test) more cats had a paw preference ($N=32$, 72.7%) than were ambilateral ($N=12$, 27.3%), however the paw-preferent cats were no more likely to be left- ($N=18$, 56.2%) than right- ($N=14$, 43.8%) pawed ($P>0.05$, binomial test) [Figure 2].

Lying side

Analysis revealed that 4 (9.1%) cats preferred to consistently lie on their left side, 7 (15.9%) preferred to lie on their right side, while 33 (75.0%) were ambilateral for this behaviour (Figure 2). This distribution of lateral bias was significantly different to that expected by chance alone ($\chi^2_2=34.68$, $P<0.001$). Significantly ($P=0.001$, binomial test) more cats were ambilateral than side-preferent, but side-preferent cats were no more likely to exhibit a left than right side preference for this behaviour ($P>0.05$, binomial test).

Step down

Fifteen (34.1%) cats were reported to consistently use their left paw to step down a flight of stairs, 16 (36.4%) to use their right paw, while 13 (29.5%) animals were ambilateral (Figure 2). This distribution of paw use did not differ significantly ($\chi^2_2=0.32$, $p=0.85$). Significantly ($P=0.010$, binomial test) more cats were paw-preferent than ambilateral for this behaviour,

however paw-preferent cats were no more likely to be left- than right-pawed ($P>0.05$, binomial test).

Step over

Sixteen (36.4%) of the subjects were reported to consistently use their left paw to step over, 13 (29.5%) to use their right paw and 15 (34.1%) showed no paw preference (Figure 2). This distribution of paw preference was not significantly different to that expected by chance alone ($\chi^2_2=0.32$, $p=0.85$). Significantly ($P=0.04$, binomial test) more cats were paw-preferent for this behaviour than ambilateral, however paw-preferent cats were no more likely to be left- than right-pawed ($P>0.05$, binomial test).

(Figure 2 about here)

Direction of lateral bias

A mixed-design ANOVA revealed no significant effect of task ($F_{3,120}=1.03$, $P=0.38$) on the direction of the cats' motor bias. This measure was significantly related to feline sex ($F_{1,40}=5.15$, $P=0.02$), with males favouring their left side (mean HI= 0.15 +/- 0.07) and females preferring their right side (mean HI= -0.12 +/- 0.07). The age of the cats was unrelated to the direction of the animals' motor bias ($F_{1,40}=0.11$, $P=0.74$).

There was a significant positive correlation in the direction of the cats' lateral bias between the *food reaching* test and all of the three spontaneous behaviours [P values corrected for multiple comparisons] (*lying side*, $R_{44}=0.38$, C.I.=0.09-0.67, $P<0.05$, *step down*, $R_{44}=0.61$, C.I.=0.37-0.86, $P<0.001$, *step over*, $R_{44}=0.54$, C.I.=0.28-0.80, $P<0.001$). HI scores for the *step down* and *step over* tests were also significantly correlated ($R_{44}=0.58$, C.I.=0.33-0.84,

$P<0.001$). There was no significant correlation in the direction of the cats' motor preferences for behaviours of *lying side* and *step down* ($R_{44}=0.28$, C.I.=-0.02-0.58, $P=0.06$) or *step over* ($R_{44}=0.25$, C.I.=-0.48-0.13, $P=0.10$).

Strength of lateral bias

The strength of the cats' lateral bias differed significantly between the tasks ($F_{3,120}=4.49$, $P=0.005$). Post-hoc paired t -tests (with P values corrected for multiple comparisons) showed that cats displayed a significantly weaker lateral bias for *lying side* (mean ABS-HI= 0.20 +/- 0.02) than for *food reaching* ($t_{43}=7.09$, $P<0.001$; mean ABS-HI= 0.50 +/- 0.04), *step down* ($t_{43}=7.09$, $P<0.001$; mean ABS-HI= 0.44 +/- 0.03) and *step over* ($t_{43}=-4.5$, $P<0.001$; mean ABS-HI= 0.40 +/- 0.04).

Analysis revealed no significant effect of feline sex ($F_{1,40}=0.31$, $P=0.58$) or age ($F_{1,40}=0.31$, $P=0.85$) on the strength of the animals' lateral bias

There was a significant positive correlation in the strength of the cats' paw use for the behaviours of *step down* and *step over* ($R_{44}=0.50$, C.I.=0.22-0.76, $P<0.001$). None of the other behaviours were significantly correlated for strength of motor bias ($P>0.05$).

DISCUSSION

The results from this study provide the first evidence that certain spontaneous behaviours, notably those involving limb use, are lateralised in the domestic cat. The study also suggests that food reaching tests, commonly used to assess paw preference in the cat, offer an ecologically valid measure of laterality for this species.

The majority of cats in the present study showed a lateral bias on the measures involving paw use, i.e., *food reaching* (73%), *step down* (70%) and *step over* (66%). Paw-preferent animals, however, did not differ significantly in their tendency towards left- or right-sidedness. Previous studies have reported a roughly similar distribution of lateralisation in cats tested on a range of challenges designed to assess paw preference (Pike & Maitland, 1997; Tan & Kutlu, 1991; Tan, Yaprak & Kutlu, 1990; Wells & Millsopp, 2009, 2012), and, together, point strongly to paw use at the level of the individual for this species. The spontaneous behaviour of *lying side*, the only measure that did not concentrate on paw use, was not found to be lateralised, with only 25% of the subjects exhibiting a significant side preference for this activity. With this in mind, future studies on feline laterality may be wiser to focus their attention on behaviours involving limb use, which appear to be more reflective of hemispheric specialisation in the cat.

The cats' HI scores were found to be significantly correlated for most of the measures in this study, whether forced or spontaneous. Previous experiments have yielded mixed results regarding the consistency of motor bias on experimental tasks *vs.* expressions of spontaneous behaviours, with some authors pointing to a significant relationship between such measures (Chapelain et al., 2012), and yet others unearthing no evidence of an association (Chapelain et al., 2006; Schnoell et al., 2014). Much appears to depend on the nature of the measures

under scrutiny. Studies which have isolated a specific spontaneous action have reported more consistent patterns of motor bias between experimental tasks and natural behaviours than those that have combined very different actions. For instance, Chapelain and associates (2012) found consistency in reaching for an object (food) both spontaneously and in a more forced experimental set-up in both red-capped mangabeys and Campbell's monkeys. By contrast, Schnoell and colleagues (2014) reported no consistency in the hand use of red-fronted lemurs on a forced food reaching task compared to the expression of 5 spontaneous actions, e.g., allogrooming, autogrooming, warding off conspecifics. It may be more beneficial and methodologically valid to focus on one specific spontaneous behaviour to get a clearer representation of natural laterality, although deciding on an adequate measure has proven difficult (e.g., Marchant & McGrew, 1996). Studies on primates have shown that animals often only show lateralised hand use for specific spontaneous actions, e.g., feeding (Meguerditchian et al., 2010; Tabiowo & Forrester, 2013), whilst others, often those for which there is no biological value to be gained from lateralisation (e.g., lying side, as reflected in the present study), are more likely to be ambilateral in nature.

The strength of the cats' motor bias was found to be related to task, with animals displaying a significantly weaker lateral bias for *lying side* than any of the other measures. However, strength of paw preference did not differ significantly between the *food reaching*, *step down* or *step over* tests, as might have been expected. It has been argued that the synthetic nature of an experimental task can create artificially stronger motor asymmetries (Warren, 1980); limb preferences tend to be less flexible on forced tasks, and are perhaps more readily reinforced, e.g., by food treats. In a similar vein, the 'task complexity' hypothesis argues that more complex actions, which tend to demand the use of one hemisphere over the other, typically result in a stronger motor bias (Fagot & Vauclair, 1991). These theories may

explain why the cats in the present study were more weakly lateralised for the spontaneous behaviour of *lying side*, the least demanding motor challenge. However, they do not necessarily explain why the cats showed no stronger a paw preference on the food reaching task. The findings suggest that limb use on a forced experimental challenge may not be an artificial phenomenon, but may, rather, be an ecologically reliable indicator of motor bias for the domestic cat. The findings also lend support for the suggestion that task specific cues (e.g., postural support, task complexity) may not influence manual laterality in non-primate mammals (Konerding, Hedrich, Bleich, & Zimmerman, 2012).

The study revealed a sex split in the direction, although not the strength, of the cats' lateral bias on the *food reaching* task and two of the three spontaneous behaviours (*step down* and *step over*). In all cases, male animals showed a significant preference for using their left paw, while females were more inclined to exhibit a right-sided bias. This sex split has been found previously in cats (Wells & Millsopp, 2009, 2012) and other species, e.g., dogs (Quaranta, Siniscalchi, Frate & Vallortigara, 2004; Wells, 2003), horses (Murphy, Sutherland, & Arkins, 2005). It is the first time, however, that spontaneous actions have been shown to be related to feline sex. Interestingly, the few studies that have reported differences between male and female animals for naturalistic behaviours have demonstrated a directional effect similar to that observed in this experiment for some tasks (black and white snub-nosed monkeys, *Pan*, Xiao & Zhao, 2011; lemurs, Ward, Milliken, Dodson, Stafford & Wallace, 1990). It has been argued that naturalistic behaviours encouraged the evolution of cerebral specialisation for motor dominance (Forrester et al., 2013). Assuming this is the case, a sex split would not necessarily be expected for spontaneous actions. Indeed, it would be more efficient and generally advantageous for a species to demonstrate population-level laterality for

spontaneous expressions of behaviour (e.g., Ghirlanda, Frasnelli & Vallortigara, 2009; Ghirlanda & Vallortigara, 2004).

In some respects, it is surprising that a sex effect was discovered in this study, since the sample was comprised entirely of castrated animals. Studies on dogs have failed to report an effect of canine sex on paw preferences in samples of neutered, or a mixture of de-sexed and entire, animals (Batt, Batt, Baguley & McGreevy, 2008; Branson & Rogers, 2006; Schneider, Delfabbro & Burns, 2013; Wells, Hepper, Milligan & Barnard, 2017); this has led the authors to argue that a hormonal factor may be at play in shaping motor bias. Further work is needed to investigate this, but the strong sex effects reported here, and elsewhere, both on experimental challenges and expressions of spontaneous behaviour, and using both castrated and de-sexed populations, point more and more strongly to underlying differences in the neural architecture of male and female cats. This is perhaps not surprising, given the sex differences in brain asymmetries reported across species (see Bianki & Filippova, 2001).

Some authors have reported relative stability in preferred limb use across the lifespan in nonhuman species, notably primates (e.g., Hook & Rogers, 2000; Stafford, Milliken & Ward, 1990). There was no evidence from the present investigation that paw use differed between the younger and older cohorts of cat. In their earlier studies, Wells and Millsopp (2012) found that cats' paw preferences differ significantly over the course of their first year of life, stabilising thereafter. The youngest cats in the present study were 1 year of age, no doubt explaining the lack of any significant age effects. The findings from this study lend further support for the idea that cats, like others species, show stability in paw preferences across adulthood, even in the display of naturalistic behaviours.

Conclusions

The findings from this study provide the first evidence that the domestic cat displays motor laterality on specific spontaneous behaviours, notably those involving limb use, and that the direction of these lateral biases is largely consistent with that of an experimental task. The results suggest that the more forced food reaching tests traditionally used to assess motor bias in the cat offer a biologically valid measure of limb use in this species. It is clear that both context and relevance of lateralisation of particular behaviours are important factors which need to be considered when interpreting the results from investigations of this nature. However, it could be argued that exploring lateral bias on an experimental task, as well as spontaneous expressions of behaviour, may provide more realistic insights into the evolution and importance of lateral bias in an animal's daily life than the use of just one methodological approach. Future studies may also consider exploring other forms of lateral bias in addition to limb preferences as an indicator of cerebral asymmetry. Feral horses, for example, have been found to display significant eye preferences in the absence of a limb bias (Austin & Rogers, 2012), while common marmosets show a strong bias at the level of the group for eye use, but not hand preference (Hook & Rogers, 1998). Exploring lateral biases beyond limb preference may further our understanding of cerebral functioning in nonhuman species.

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591

592 **Figure Legends**

593

594 Figure 1. The Catit Food Maze used for the food-reaching test (see also
595 <https://www.catit.com/uk/shop/senses-2-food-tree>)

596

597 Figure 2. Distribution of lateral bias across the four measures

Figure 1



Figure 2

